The diving behavior of large whales: is dive duration shorter than predicted?

[a] Donald A. Croll

[a] Alejandro Acevedo-Gutiérrez

[a] Bernie R. Tershy

[b] Jorge Urbán-Ramírez

[a] *Institute of Marine Sciences, A316 Earth and Marine Sciences Bldg., University of California, Santa Cruz, CA 95064, USA*

[b] *Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, A.P. 19-B, 23080 La Paz, BCS, México*

Correspondence: Donald A. Croll; Institute of Marine Sciences, A316 Earth and Marine Sciences Bldg., University of California, Santa Cruz, CA 95064, USA; phone: 1 (831) 459 3610; fax: 1 (831) 459 4882; dcroll@cats.ucsc.edu

Running title: Aerobic dive limit and large whales

Abstract

Most diving seabirds and marine mammals have been found to regularly exceed their theoretical aerobic dive limit (TADL). No animals have been found to consistently dive for durations that are significantly shorter than their TADL. We attached time-depth recorders to seven blue whales and fifteen fin whales (family Balaenopteridae). The diving behavior of both species was similar, and we distinguished between foraging and traveling dives. Foraging dives in both species were deeper, longer in duration, and distinguished by a series of vertical excursions where lunge feeding presumably occurred. Foraging blue whales lunged 2.4 (± 1.13) times per dive, with a maximum of six times, and average vertical excursion of 30.2 (± 10.04 m). Foraging fin whales lunged 1.7 (± 0.88) times per dive, with a maximum of eight times, and average vertical excursion of 21.2 (± 4.35 m). The maximum rate of ascent of lunges was higher than the maximum rate of descent in both species, indicating that feeding lunges occurred on ascent. Foraging dives were deeper and longer than non-feeding dives in both species. On average, blue whales dived to 140.0 (± 46.01) m and 7.8 (± 1.89) min when foraging, and 67.6 (±51.46) m and 4.9 (±2.53) min when not foraging. Fin whales dived to 97.9 (±32.59) m and 6.3 (±1.53) min when foraging and to 59.3 (±29.67) m and 4.2 (±1.67) min when not foraging.

The longest dives recorded for both species: 14.7 min for blue whales and 16.9 min for fin whales were considerably shorter than the TADL of 31.2 and 28.6 min, respectively. An allometric comparison of marine mammals diving to an average depth of 80-150 m indicated that Balaenopteridae whales, with a mean dive duration of 6.8 min, dived for durations that were 10.7 min shorter than predicted. Thus the short dive durations of blue whales and fin whales cannot be explained by the shallow distribution of their prey. We propose instead that short duration diving in large whales results from either: 1) dispersal behavior of prey, or 2) a high energetic cost of foraging.

Keyword(s): Diving; Aerobic dive limit; Blue whale; Fin whale; Foraging; *Balaenoptera*

Introduction

Blue whales (*Balaenoptera musculus*) and fin whales (*B. physalus*) are the largest animals on earth. Adult blue whales average 24.7 m in length and 92,671 kg in weight (Nishiwaki 1950). Fin whales average 21.2 m in length and 52,584 kg in weight (Nishiwaki 1950). As with the rest of baleen whales, the two species feed by filtering prey through baleen plates that hang from the roof of the mouth. However blue whales and fin whales capture their prey by lunge feeding. During a lunge, rorquals capture food by swimming rapidly at a prey school and opening the mouth to engulf large quantities of water and schooling prey as the tongue moves downward and backward (Kawamura 1980; Lambersten 1983). Blue whales feed almost exclusively on euphasiid crustaceans while fin whales feed on planktonic crustaceans, including euphasiids, and pelagic shoaling fish (Kawamura 1980). Due to their large size, baleen whales require large concentrations of food (Brodie et al. 1978; Macaulay et al. 1995; Wishner et al. 1995). Thus, blue whales feed on dense aggregations of euphasiids, at least two orders of magnitude greater than background levels (Croll et al. in rev.).

An animal that dives to forage must return to the surface before its O_2 reserves are exhausted, assuming that it makes an aerobic dive (Houston and Carbone 1992; Boyd 1997). Thus large animals should dive longer than small animals since oxygen stores increase and mass-specific metabolic rate decrease with body size (Costa 1991). This relationship between mass specific oxygen stores and diving metabolic rate has led to the development of the concept of the aerobic dive limit (Kooyman et al. 1980). The aerobic dive limit (ADL) is defined as “the maximum breath-hold that is possible without an increase in the blood lactic acid concentration during or after a dive”. The theoretical aerobic dive limit (TADL) is thus calculated by estimating the O_2 stores and diving metabolic rate of a species, usually based upon body mass (Kooyman 1989). While Boyd and Croxall (1996) and Boyd (1997) have found that many seabirds and some pinnipeds routinely exceed this limit, few field-based studies have described diving behavior where dive duration are typically much less than the TADL.

Baleen whales dive to shallower depths and for shorter periods than would be predicted from an allometric consideration of their body size (Schreer and Kovacs 1997). This has been explained as a consequence of prey being found in relatively shallow waters (Schreer and Kovacs 1997). In a general sense, theoretical models support this explanation, but such arguments have never been applied to the largest diving animals (blue and fin whales) using field measurements of diving behavior. Recent studies that have measured the depth distribution of the euphausiid prey of large whales have shown that large euphasiid concentrations that are important in the diet of blue and fin whales are typically found at depths exceeding 100 m (Sardou et al 1996; Croll et al. 1998; Croll et al. in rev.). Furthermore, if blue and fin whales dive for short periods of time because their prey is located at shallow depths, foraging theory would predict that their dive times should be longer than that of smaller species that are smaller in size yet diving to a similar depth. Here we 1) describe the foraging and non-foraging dive behavior of blue whales and fin whales, 2) relate body mass and dive time of several families of divers in which individuals dive to depths close to 100-150m, and 3) calculate the TADL of blue whales and fin whales, and compare it to field measurements of their dive times.

Materials and Methods

Data collection

The diving behavior of seven blue whales and fifteen fin whales was measured between 1995 and 1999 using attached time-depth recorder packages (Tables 1, 2). Recorders remained attached for 5.7 ± SD 3.10 h in blue whales and 14.4 ± SD 9.36 h in fin whales. Whales were tagged in Bahia de La Paz, Mexico (24°30’N, 110°30’W); Bahia de Loreto, Mexico (25°42’N, 111°09’W); Monterey Bay, USA (35°34’N, 112°00’W); and the Channel Islands, USA (34°00’N, 120°30’W).

The tags and methodology employed to attach them are described in Croll et al. (1998). Briefly, tags were attached to the dorsal surface of the whale 2 – 3 m caudal of the blowhole using a compound crossbow. They were deployed from a small skiff (< 7 m). Each tag had three components: 1) a Wildlife Computers (Redmond, Washington) Mk 5 time/depth/temperature recording device (TDR), 2) a VHF radio transmitter (Advance Telemetry Systems, Isanti, Minnesota) to track the tagged whale, and 3) a radio activated release mechanism (Jamie Stamps, Livermore, California). Time, depth, and temperature were logged at 1-s intervals. Upon tagging each whale was followed in a 15-m vessel at a distance of 100-200 m. The behavior of each tagged whale was observed and recorded every surface interval. We recorded location, direction of movement, and proximity of conspecifics. Once the tag was released from the whale, we localized it using the directional VHF system.

Data analysis

Dive data were analyzed using software provided by the TDR manufacturer (Dive Analysis, Wildlife Computers). We considered each individual whale an independent observation and calculated median values for dive parameters for individual whales. These median values were then averaged across whales to produce mean values for each species. Dives were defined as submergences that exceeded 20 m in depth. We report dive depth as the maximum depth that a whale reached during a dive. The program recorded maximum rates of ascent and descent when whales were lunging (defined below) and when they were traveling to and from the surface. We call the latter rates of ascent and descent of the dive. These rates were measured in m s^{-1} and are likely underestimates because the program assumes that whales moved at a 90° angle with respect to the surface of the water. Visual inspection of the dive profile revealed that whales often made a series of ascending and descending vertical excursions exceeding 8m during the dive. We defined each excursion as a foraging lunge and estimated the number of lunges for each dive.

Dive behavior- Whales were considered to be foraging if the profile of time versus depth in the computer showed one or more lunges during the dive (Figs. 1a, 2a), and non-foraging if no lunges were recorded (Figs. 1b, 2b). We compared dive depth and dive time between foraging and non-foraging dives of individual whales with a paired-sample t test (Zar 1996). Because we conducted two different tests significance was assessed at $p = 0.03$. We also compared the speed of ascent and descent of lunges between foraging and non-foraging whales with a paired-sample t test (Zar 1996). We compared occurrence of foraging dives and dive depth according to time of day with a paired-sample t test (Zar 1996). Because we conducted two different tests significance was assessed at $p = 0.03$.

Dive time vs. body mass- To examine allometric relationship between dive duration and body mass across taxonomic groups of divers, we averaged the dive times of species belonging to the same family. We only analyzed studies in which the species dove to a depth of 80-150 m to ensure that differences in the duration of the dive were not related to differences in the depth of the dive. A regression of body mass and dive time was conducted between the following families: Sphenisciidae, Otariidae, Phocidae, Ziphiidae, and Monodontidae. From the fitted curve we estimated the predicted dive time of an animal having the same mass of a Balaenopteridae whale (average mass of blue, fin and humpback whales; Table 3). We also estimated the predicted dive time of an animal having the same mass of a Balaenidae whale (average mass of right and bowhead whales), which is similar to the body mass of blue whales and fin whales (Table 3).

Theoretical aerobic dive limit (TADL)- We compared dive durations with calculated TADLs (Boyd and Croxall 1996). The TADLs of blue whales and fin whales were calculated following the methodology described by Kooyman (1989). We estimated oxygen stores based on published values from other marine mammals (Table 4) and the methodology of Shaffer et al. (1997). Basal metabolic rate was calculated from the allometric equation of Kleiber (1961), and we utilized 4 x BMR as an estimate of diving metabolic rate when foraging underwater following the convention of Boyd and Croxall (1996). Marine mammals, including blue whales, extend their aerobic dive time by gliding underwater (Williams et al. 2000). In Wedell seals (*Leptonychotes wedelli*) the reduction in oxygen consumption due to this behavior averages 27.8 % (Williams et al. 2000). We assumed a similar reduction in recovery oxygen consumption for blue whales and fin whales (Table 4).

Results

We recorded 231 dives from seven tagged blue whales (Table 1). The maximum dive depth was 204 m and the maximum duration of a dive was 14.7 min. We recorded 1152 dives from 15 tagged fin whales (Table 2). The maximum dive depth was 306 m and the maximum duration of a dive was 16.9 min.

Dive behavior

Foraging dives were deeper and longer than non-feeding dives in both blue and fin whales (Figs. 2, 3). Blue whales dove to 140.0 ± SD 46.01 m when foraging and to 67.6 ± SD 51.46 m when not foraging (paired-t test: $t_6 = 3.25$, $p = 0.017$, Fig. 3a). They dove for 7.8 ± SD 1.89 min when foraging and for 4.9 ± SD 2.53 min when not foraging (paired-t test: $t_6 = 2.91$, $p = 0.027$, Fig. 3b). Fin whales dove to 97.9 ± SD 32.59 m when foraging and to 59.3 ± SD 29.67 m when not foraging (paired-t test: $t_{14} = 4.46$, $p < 0.001$; Fig. 4a). They dove for 6.3 ± SD 1.53 min when foraging and for 4.2 ± SD 1.67 min when not foraging (paired-t test: $t_{14} = 8.22$, $p < 0.001$, Fig. 4b).

Foraging blue whales lunged 2.4 ± SD 1.13 times, with a maximum of six times; foraging fin whales lunged 1.7 ± SD 0.88 times, with a maximum of eight times (n = 7 blue whales and 15 fin whales). Vertical excursions during lunges averaged 30.2 ± SD 10.04 m in blue whales and 21.2 ± SD 4.35 m in fin whales (n = 7 blue whales and 15 fin whales). The maximum rate of ascent of lunges was higher than their maximum rate of descent (paired-t test, blue whales: $t_6 = 2.95$, $p = 0.026$, Table 1; fin whales: $t_{14} = 2.80$, $p = 0.014$, Table 2).

Dive time vs. body mass

There was a positive relationship between dive time and body mass in the five taxonomic families analyzed ($r^2 = 0.80$, $F_{1,3} = 16.58$, $p = 0.027$, Fig. 7). The observed dive time of the family Balaenopteridae (6.9 min – including humpback whales) was 10.7 min below the predicted value for an animal with their body mass (62,217 kg). If we include the family Balaenopteridae in the regression, the coefficient drops significantly ($r^2 = 0.11$, $F_{1,4} = 1.59$, $p = 0.276$). In contrast, the observed dive time of the family Balaenidae (15.3 min) was 2.1 min below the predicted value for an animal with their body mass (60,605 kg). If we include the family Balaenidae in the regression, the coefficient raises notably ($r^2 = 0.85$, $F_{1,4} = 28.83$, $p = 0.006$).

Theoretical aerobic dive limit (TADL)

Dive duration as a proportion of the TADL followed a unimodal distribution in both blue whales and fin whales (Fig. 8a, 8b). The median dive time represented 19% and 17% of the TADL in blue whales and fin whales, respectively. The longest dive observed represented 47% of the TADL in blue whales and 59% in fin whales.

Discussion

Foraging dives were longer and deeper than non-foraging dives in both blue whales and fin whales (Figs. 3-6). The depth of foraging dives we measured was related to the depth at which prey were concentrated (Croll et al. 1998). Our data also indicate that blue whales and fin whales fed mostly at depth and rarely at the surface, which highlights the importance of remote-sensing techniques to understand the behavior of whales. The higher rates of ascent vs. descent during lunges suggest that prey capture generally takes place during the ascending portion of the lunge. Under this scenario, whales may perform several foraging lunges during an individual dive, and whales close their mouths and expel water during the descending portion of the lunge (with little need for fast swimming during descent). This framework is also consistent with observations of blue whales gliding during the descent part of a lunge (Williams et al. 2000).

Blue whales and fin whales did not dive for long periods of time. The maximum dive times we recorded for blue whales and fin whales (14.7 and 16.9 min, respectively) are similar to those reported in the literature: blue whales 16.4 – 26.9 min (Donovan 1984; Strong 1990; Lagerquist et al 2000), fin whales 12.6- 25.9 min (Strong 1990; Panigada et al. 1999). Unlike all species of diver studied to date, blue and fin whales never exceeded their TADL of 31.2 and 28.6 min respectively. Anecdotal evidence indicates that blue whales and fin whales are able to dive for as long as 50 and 30 min, respectively (Leatherwood et al. 1982). However these appear to be cases in which whales found themselves in life-threatening situations (Leatherwood et al. 1982). In contrast, most seabirds and some pinniped species regularly exceed their TADL (Boyd and Croxall 1996; Boyd 1997). Even species that usually dive below their TADL, such as the Antarctic fur seal (*Arctocephalus gazella*), occasionally exceed this limit (Boyd and Croxall 1996).

Why do Balaenopteridae whales dive for durations so much less than their TADL? Comparison of dive depth with the reported depth distribution of prey does not support the hypothesis that Balaenopteridae whales dive for short durations due to the shallow distribution of their prey as it is generally found in depths exceeding 100m (Croll et al. 1998, Croll et al. in press). Two possibilities may explain the short duration of dives in comparison with the TADL for large whales: 1) dispersal of prey during foraging lunges leads to sub-optimal densities of prey during the course of a foraging dive, or 2) we have underestimated the metabolic cost of foraging lunges in our calculation of TADL. We believe that a high cost of lunging is the most likely explanation because hydroacoustic measurement of euphausiid densities in the presence of foraging whales do not indicate reduced prey densities (Croll et al. 1998). Furthermore, the rapid swimming necessary for successful lunge feeding is likely energetically costly and thus would deplete oxygen stores and reduce dive time (Costa 1991). A similar explanation has been proposed to explain foraging dives in Antarctic fur seals, which appear to dive with a high metabolic rate (Boyd et al. 1995) and rarely exceed their TADL (Boyd and Croxall 1996). The argument that lunging is a costly behavior would also explain the discrepancies between rorquals and right whales when diving at similar depths (Fig. 7). Right whales move slowly while skimming small planktonic prey through the water column (Pivorunas 1979). Their speed at the bottom averages 0.7 $m \cdot s^{-1}$ (Goodyear 1995) and their foraging dives lasts up to 30 min (Würsig and Clark 1993). We hypothesize that foraging costs are low in right whales, allowing them to forage for longer periods underwater on prey which is not as densely aggregated, and high in Balaenopteridae whales, forcing them to forage for relatively short periods.

Acknowledgments

We thank our many field assistants and vessel crews for their dedication and support. The Monterey Bay and Channel Islands National Marine Sanctuaries, and Parque Nacional Bahia Loreto, Mexico provided logistic support. Funding was provided by Office of Naval Research Grants N00014-95-10646 and N00014-99-10192 to D. Croll, National Oceanic and Atmospheric Administration Contracts 40ABNC602168 and 40ABNF600916 to D. Croll and B. Tershy, National Oceanic and Atmospheric Administration Contract 50ABNF500153 to D. Costa, D. Croll, T. Williams, and J. Harvey, and Scripps Institution of Oceanography ARPA MDA 972-93-1-003 to D. Costa. Thanks to S. Noren and S. Shaffer for providing information for the calculation of TADLs.

Literature Cited

Benjaminsen, T., Christensen, I., 1979. The natural history of the bottlenose whale Hyperoodon ampullatus. In: Winn, H.E., Olla, L.B. (Eds.) Behavior of Marine Animals, vol. 3. Cetaceans. Plenum Press, New York, pp.143-164.

Boyd, I.L., 1997. The behavioural and physiological ecology of diving. TREE 12, 213-217.

Boyd, I.L., Croxall. J.P., 1996. Dive durations in pinnipeds and seabirds. Can. J. Zool. 74, 1696-1705.

Boyd, I.L., Reid, K., Bevan, R.M., 1995. Swimming speed and allocation of time during the dive cycles in Antarctic fur seals. Anim. Behav. 50, 769-784.

Brodie, P.F., 1989. The white whale Delphinapterus leucas (Pallas, 1776). In: Ridgway, S.H., Harrison, R. (Eds.) Handbook of Marine Mammals, vol. 4. River Dolphins and the Larger Toothed Whales. Academic Press, San Diego, pp. 119-144.

Brodie, P.F., Sameoto, D.D., Shelkdon, R.W., 1978. Population densities of euphasiids off Nova Scotia as indicated by net samples, whale stomach contents, and sonar. Limnol. Oceanogr. 23, 1264-1267.

Campagna, C., Fedak, M.A., McConnell, B.J., 1999. Post-breeding distribution and diving behavior of adult male southern elephant seals from Patagonia. J. Mammal. 80, 1341-1352.

Castellini, M.A., Kooyman, G.L., Ponganis, P.J., 1992. Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. J. Exp. Biol. 165, 181-194.

Costa, D.P., 1991. Reproductive and foraging energetics of pinnipeds: implications for life history patterns. In: Renouf, D. (Ed.) The Behavior of Pinnipeds. Chapman and Hall, London, pp. 300-344.

Croll, D.A., Tershy, B.R., Hewitt, R.P., Demer, D.A., Fiedler, P.C., Smith, S.E., Armstrong, W., Popp, J.M., Kiekhefer, T., Lopez, V.R., Urbán, J., Gendron, D., 1998. An integrated approach to the foraging ecology of marine birds and mammals. Deep-Sea. Res. II 45, 1353-1371.

Croll, D.A.,Clark, C.P., Calambokidis, J., Ellison, W.T., Tershy, B.R., in press. Effect of anthropogenic low frequency noise on the foraging ecology of Balaenoptera whales. Anim. Conserv.

Croll, D.A., Marinovic, B., Benson, S., Chavez, F., Black, N., Terullo, R., Tershy, B.R., in rev. From wind to whales: trophic links in a coastal upwelling system. Ecology.

DeLong, R.L., Stewart, B.S., 1991. Diving patterns of northern elephant seal bulls. Mar. Mamm. Sci. 7, 369-384.

Deutsch, C.J., Crocker, D.E., Costa, D.P., Le Boeuf, B.J., 1994. Sex- and age-related variation in reproductive effort of northern elephant seals. In: Le Boeuf, B.J., Laws, R.M. (Eds.) Elephant Seals: Population Ecology, Behavior, and Physiology. University of California Press, Berkeley, pp. 169-210.

Dolphin,W.F., 1988. Foraging dive patterns of humpback whales, Megaptera novaeangliae, in southeast Alaska: a cost-benefit analysis. Can. J. Zool. 66, 2432-2441.

Donovan, G.P., 1984. Blue whales off Peru, December 1982, with special reference to pygmy blue whales. Rep. Int. Whal. Commn. 34, 473-476.

Dunning, J.B. Jr, (Ed.), 1993. CRC Handbook of Avian Body Masses. CRC Press, Boca Raton, FL.

Feldkamp, S.D., DeLong, R.L., Antonelis, M.A., 1989. Diving patterns of California sea lions, Zalophus californianus. Can. J. Zool. 67, 872-883.

Gales, N.J., Mattlin, R.H., 1997. Summer diving behaviour of lactating New Zealand sea lions, Phocarctos hookeri. Can. J. Zool. 75, 1695-1706.

Gentry, R.L., Kooyman, G.L., Goebel, M.E., 1986. Feeding and diving behavior of northern fur seals. In: Gentry, R.L., Kooyman, G.L. (Eds.) Fur Seals. Maternal Strategies on Land and at Sea. Princeton University Press, Princeton, pp. 61-78.

Goforth, H.W. Jr., 1986. Glycogenolytic responses and force production characteristics of a bottlenose dolphin (Tursiops truncatus), while exercising against a force transducer. Ph.D. thesis, University of California, Los Angeles, 137pp.

Goodyear, J.D., 1995. Dive behavior and the question of food limitation in right whales. In: Abstracts of the Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando, FL, 14-18 December 1995, The Society for Marine Mammalogy, pp. 148.

Hooker, S.K., Baird, R.W., 1999. Deep-diving behaviour of the northern bottlenose whale, Hyperoodon ampullatus (Cetacea : Ziphiidae). Proc. R. Soc. Lond. B 266, 671-676.

Houston, A.I., Carbone, C., 1992. The optimal allocation of time during the diving cycle. Behav. Ecol. 3, 255-265.

Kawamura, A., 1980. A review of food of balaenopterid whales. Sci. Rep. Whales. Res. Inst. 32, 155-197.

Kelly, B.P., Wartzok, D., 1996. Ringed seal diving behavior in the breeding season. Can. J. Zool. 74, 1547-1555

Kleiber, M., 1961. The Fire of Life: An Introduction to Animal Energetics. Wiley and Sons, New York, NY.

Kooyman, G.L., 1973. Respiratory adaptations in marine mammals. Am. Zool. 13, 457-468.

Kooyman, G.L., 1989. Diverse Divers: Physiology and Behavior. Springer-Verlag, Berlin.

Kooyman, G.L., Kooyman, T.G., 1995. Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. The Condor 97, 536-549.

Kooyman, G.L., Cherel, Y., Le Macho, Y., Croxall, J.D., Thorson, P.H., Ridoux, V., Kooyman, C.A., 1992. Diving behavior and energetics during foraging cycles in king penguins. Ecol. Monogr. 62, 143-163.

Kooyman, G.L., Wahrenbrock, E.A., Castellini, M.A., Davis, R.A., Sinnett, E.E., 1980. Aerobic and anaerobic metabolism during diving in Wedell seals: Evidence of preferred pathways from blood chemistry and behavior. J. Comp. Physiol. 138, 335-346.

Krutzikowsky, G.K., Mate, B., 1993. Dive behavior of bowhead whales as monitored by satellite radio-telemetry. In: Abstracts of the Tenth Biennial Conference on the Biology of Marine Mammals, Galveston, TX, 11-15 November 1993, The Society for Marine Mammalogy, pp. 130.

Lagerquist, B.A., Stafford, K.M., Mate, B.R., 2000. Dive characteristics of satellite-monitored blue whales (Balaenoptera musculus) off the central California coast. Mar. Mamm. Sci. 16, 375-391.

Lambertsen, R.H., 1983. Internal mechanism of rorqual feeding. J. Mammal. 64, 76-88.

Leatherwood, S., Goodrich, K., Kinter, A.L., Truppo, R.M., 1982. Respiration patterns and 'sightability' of whales. Rep. Int. Whal. Commn. 32, 601-613.

Lenfant, C., Johansen, K., Torrance, J.D., 1970. Gas transport and oxygen storage capacity in some pinnipeds and the Sea Otter. Respir. Physiol. 9, 277-286.

Ling, J.K., Bryden, M.M., 1981. Southern elephant seal Mirounga leonina Linnaeus, 1758. In: Ridgway, S.H., Harrison, R. (Eds.) Handbook of Marine Mammals, vol. 2. Seals. Academic Press, San Diego, pp. 297-327.

Lockyer, C., 1976. Body weights of some species of large whales. J. Cons. int. Explor. Mer. 36, 259-273.

Macaulay, M.C., Wishner, K.F., Daly, K.L., 1995. Acoustic scattering from zooplankton and micronekton in relation to a whale feeding site near Georges Bank and Cape Cod. Cont. Self. Res. 15, 509-537.

Mattlin, R.H., Gales, N.J., Costa, D.P., 1998. Seasonal dive behaviour of lactating New Zealand fur seals (Arctocephaus forsteri). Can. J. Zool. 76, 350-360.

Martin, A.R., Smith, T.G., 1992. Deep diving in wild, free-ranging beluga whales, Delphinapterus leucas. Can. J. Fish. Aquat. Sci. 49, 462-466.

Nerini, M.K., Braham, H.W., Marquette, W.M., Rugh, D.J., 1984. Life history of the bowhead whale, Balaena mysticetus (Mammalia: Cetacea). J. Zool. (Lond.) 204, 443-468.

Nishiwaki, M., 1950. On the body weights of whales. Sci. Rep. Whales. Res. Inst. 4, 184-209.

Noren, S.R., 1997. Oxygen stores and acid buffering capacities of cetacean skeletal muscle: A hierarchy for maximum dive duration. M.Sc. thesis, University of California, Santa Cruz. 70pp.

Odell, D.K., 1981. California sea lion Zalophus californianus (Lesson, 1828). In: Ridgway, S.H., Harrison, R. (Eds.) Handbook of Marine Mammals, vol. 1. The Walrus, Sea Lions, Fur Seals and Sea Otter. Academic Press, San Diego, pp. 67-97.

Omura, H., Ohsumi, S., Nemoto, T., Nasu, K., Kasuya, T., 1969. Black right whales in the North Pacific. Sci. Rep. Whales. Res. Inst. 21, 1-78.

Panigada, S., Zanardelli, M., Canese, S., Jahoda, M., 1999. How deep can baleen whales dive? Mar. Ecol. Prog. Ser. 187, 309-311.

Pivorunas, A., 1979. The feeding mechanisms of baleen whales. Am. Sci. 67, 432-440.

Ridgway, S.H., Bowersm C.A., Miller, D., Schultz, M.L., Jacobs, C.A., Dooley, C.A., 1984. Diving and blood oxygen in the white whale. Can. J. Zool. 62, 2349-2351.

Sardou, J., Etienne, M., Andersen, V., 1996. Seasonal abundance and vertical distributions of macroplankton and micronekton in the Northwestern Mediterranean Sea. Oceanol. Acta 19, 645-656.

Schreer, J.F., Kovacs, K.M., 1997. Allometry of diving capacity in air-breathing vertebrates. Can. J. Zool. 75, 339-358.

Schreer, J.F., Testa, J.W., 1996. Classification of Weddell seal diving behavior. Mar. Mamm. Sci. 12, 227-250.

Shaffer, S.A., Costa, D.P., Williams, T.M., Ridgway, S.H., 1997. Diving and swimming performance of white whales, Delphinapterus leucas: an assessment of plasma lactate and blood gas levels and respiratory rates. J. Exp. Biol. 200, 3091-3099.

Strong, C.S., 1990. Ventilation patterns and behavior of Balaenopterid whales in the Gulf of California, Mexico. M.Sc. thesis, Moss Landing Marine Laboratories, California State University, Moss Landing, 49pp.

Wilkens, P., York, A.E., 1997. Comparative population dynamics of fur seals. Mar. Mamm. Sci. 13, 241-292.

Williams, T.D., Briggs, D.R., Croxall, J.P., Naito, Y., Kato, A., 1992. Diving pattern and performance in relation to foraging ecology in the gentoo penguin, Pygoscelis papua. J. Zool. (Lond.) 227, 211-230.

Williams, T.M., Davis, R.W., Fuiman, L.A., Francis, J., Le Boeuf, B.J., Horning, M., Calambokidis, J., Croll, D.A., 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. Science 288, 133-136.

Wishner, K.F., Schoenherr, J.R., Beardsley, R., Chen, C., 1995. Abundance, distribution, and population structure of the copepod Calanus finmarchicus in a springtime right whale feeding area in the southwestern Gulf of Maine. Cont. Self Res. 15, 475-507.

Würsig, B., Clark, C., 1993. Behavior. In: Burns, J.H., Montague, J.J., Cowles, C.J. (Eds.) The Bowhead Whale. Special Publication Number 2, The Society for Marine Mammalogy, Allen Press, Lawrence, pp. 157-199.

Zar, J.H., 1996. Biostatistical Analysis. 3rd edn. Prentice-Hall, Inglewood Cliffs, NJ.

Figure Legends

Fig. 1- A) A series of foraging dives made by a blue whale. The spikes at the bottom of the dive are interpreted as lunges.

B) A series of non-foraging dives made by a blue whale.

Fig. 2- A) A series of foraging dives made by a fin whale. The spikes at the bottom of the dive are interpreted as lunges.

B) A series of non-foraging dives made by a fin whale.

Fig. 3- A) Frequency distribution of depth of dive in blue whales relative to behavior.

B) Frequency distribution of duration of dive in blue whales relative to behavior.

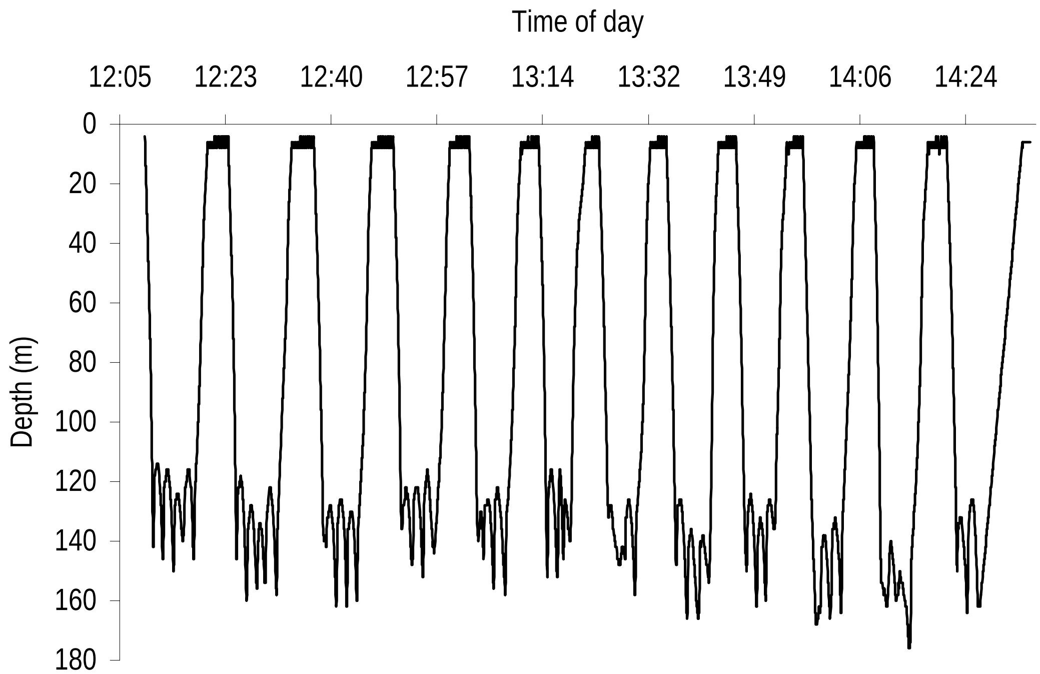
Fig. 4- A) Frequency distribution of depth of dive in fin whales relative to behavior.

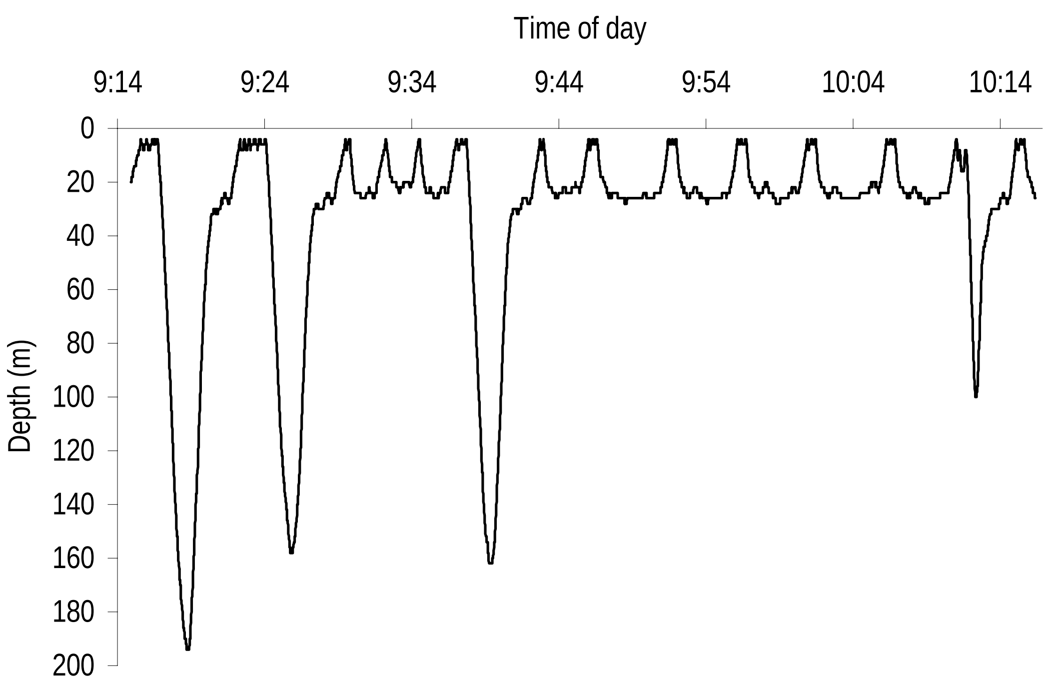
B) Frequency distribution of duration of dive in fin whales relative to behavior.

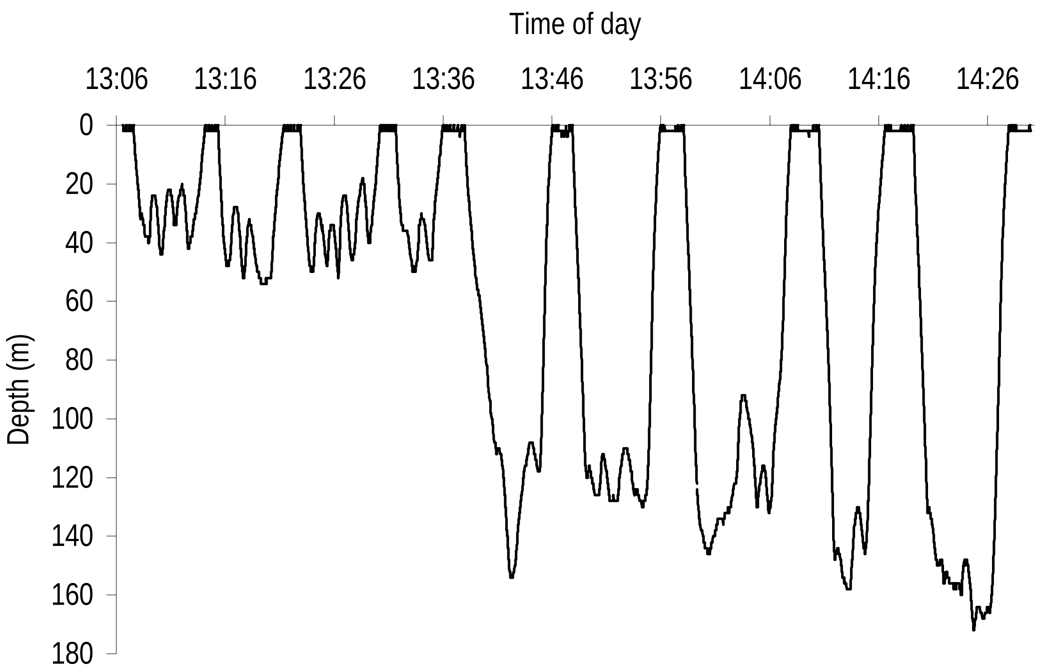
Fig. 5- Relationship between body mass and dive time of animals diving to an average depth of 80-150 m. Fitted curve: y = -2.946 + x1.847 (excluding Balaenidae and Balaenopteridae). Values and references are listed in Table 3.

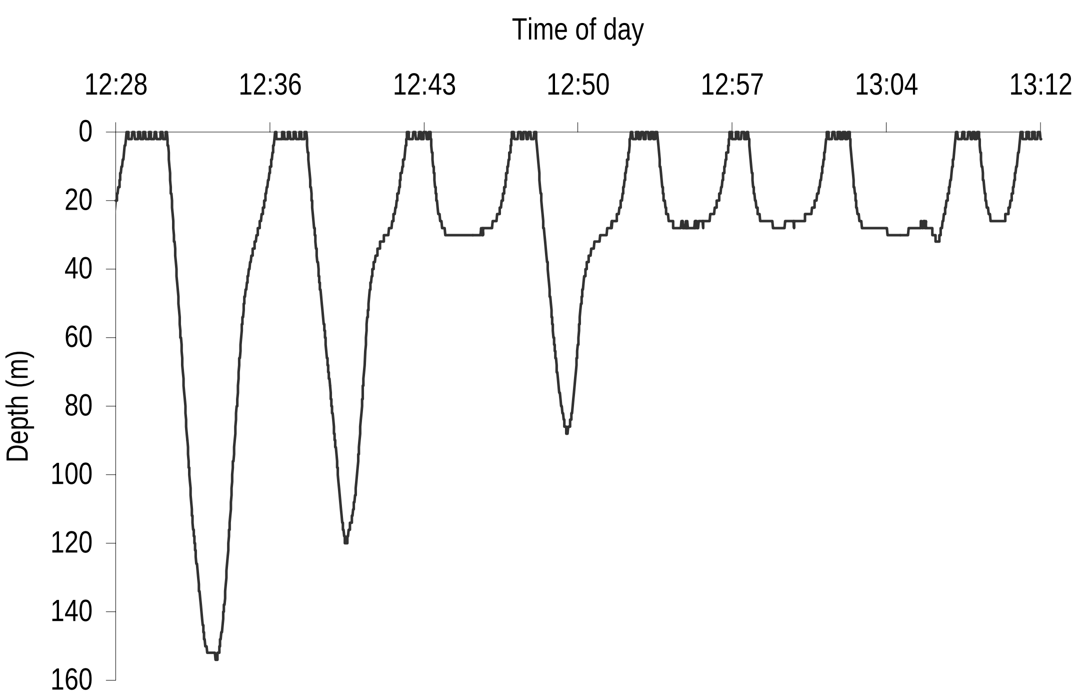
Fig. 6- A) Frequency distribution of duration of dive in blue whales relative to the theoretical aerobic dive limit (TADL).

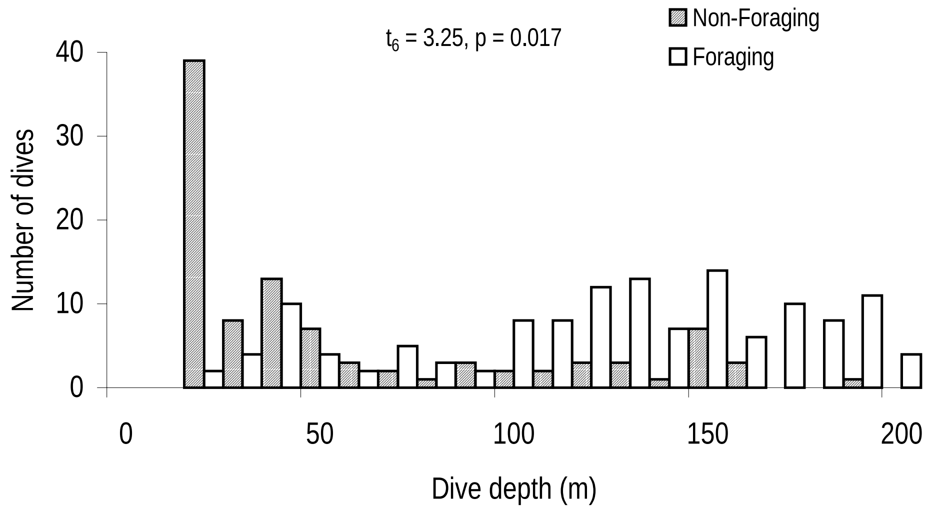
B) Frequency distribution of duration of dive in fin whales relative to TADL.

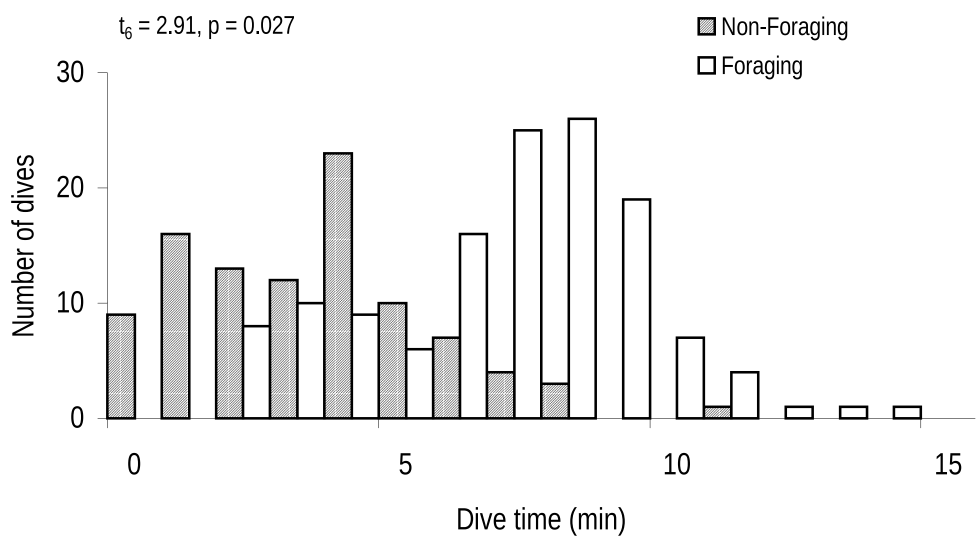

Time of day
12:05
12:23
12:40
12:57
13:14
13:32
13:49
14:06
14:24
Depth (m)
0
20
40
60
80
100
120
140
160
180

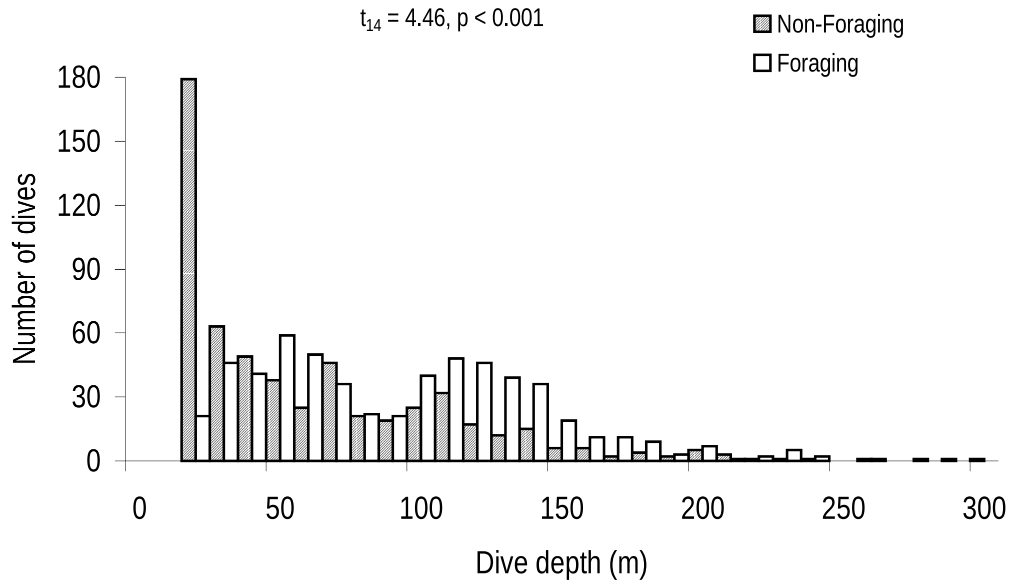

Time of day
9:14
9:24
9:34
9:44
9:54
10:04
10:14
Depth (m)
0
20
40
60
80
100
120
140
160
180
200


Time of day
13:06
13:16
13:26
13:36
13:46
13:56
14:06
14:16
14:26
Depth (m)
0
20
40
60
80
100
120
140
160
180

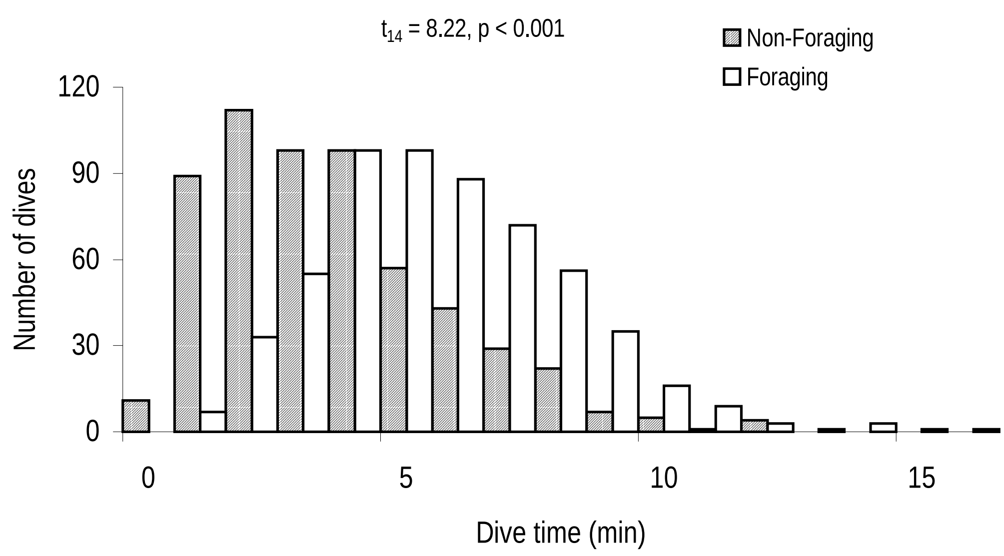

Time of day
12:28
12:36
12:43
12:50
12:57
13:04
13:12
Depth (m)
0
20
40
60
80
100
120
140
160


t6 = 3.25, p = 0.017
Non-Foraging
Foraging
40
30
20
10
0
Number of dives
0
50
100
150
200
Dive depth (m)

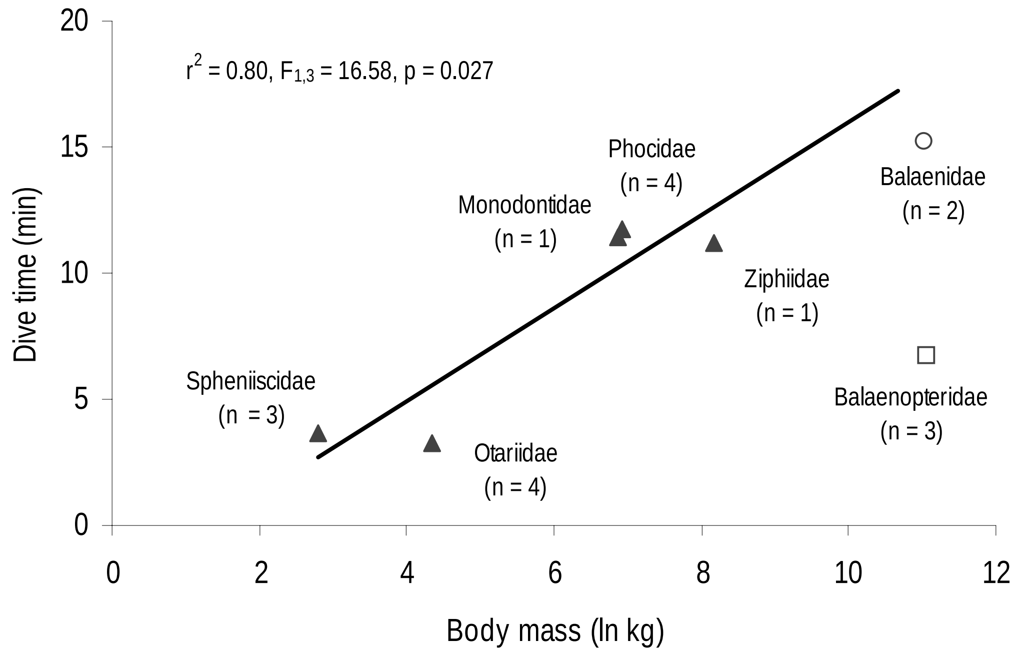

t6 = 2.91, p = 0.027
Non-Foraging
Foraging
30
20
10
0
Number of dives
0
5
10
15
Dive time (min)



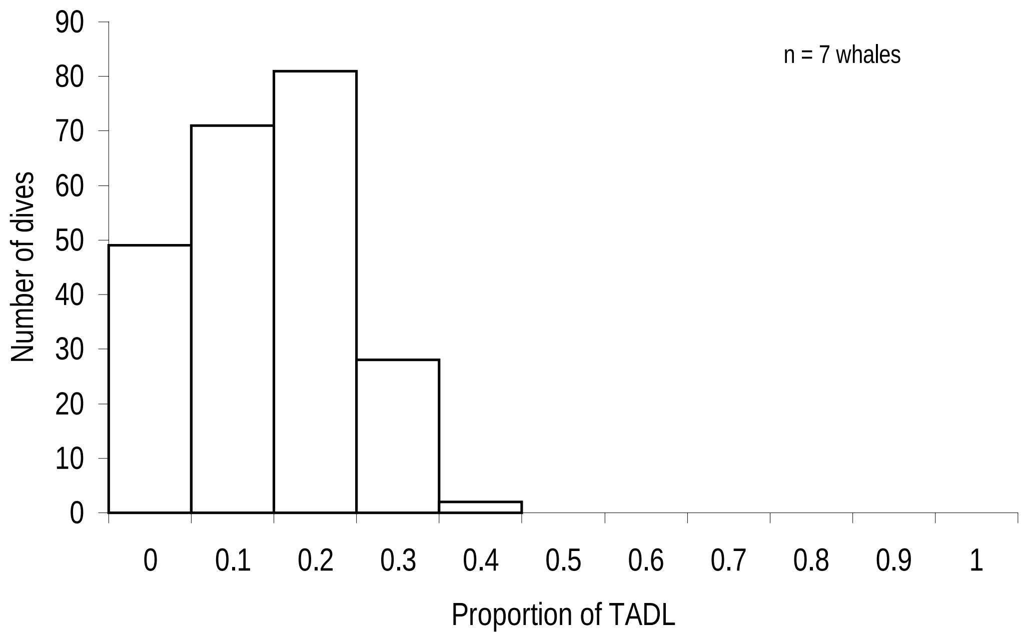
t_{14} = 4.46, p < 0.001
Non-Foraging
Foraging
Number of dives
180
150
120
90
60
30
0
0
50
100
150
200
250
300
Dive depth (m)



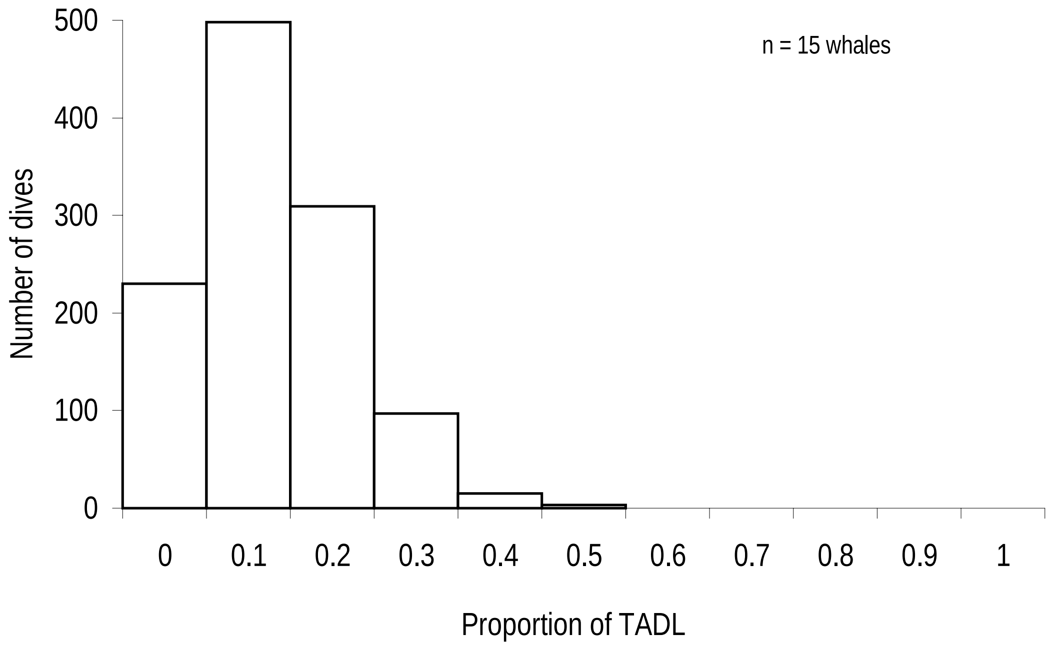
t_{14} = 8.22, p < 0.001
Non-Foraging
Foraging
Number of dives
120
90
60
30
0
0
5
10
15
Dive time (min)



20
15
10
5
0
Dive time (min)
r2 = 0.80, F1,3 = 16.58, p = 0.027
Phocidae
(n = 4)
Monodontidae
(n = 1)
Balaenidae
(n = 2)
Ziphiidae
(n = 1)
Spheniiscidae
(n = 3)
Balaenopteridae
(n = 3)
Otariidae
(n = 4)
0
2
4
6
8
10
12
Body mass (ln kg)



n = 7 whales
Number of dives
90
80
70
60
50
40
30
20
10
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Proportion of TADL



n = 15 whales
Number of dives
500
400
300
200
100
0
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
Proportion of TADL